Dendrochronologia 95 (2026) 126469

Contents lists available at ScienceDirect

Dendrochronologia

journal homepage: www.elsevier.com/locate/dendro

Warming drives non-stationary climate-growth relationships and differential drought sensitivity in Mediterranean pines

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ARTICLE INFO

Keywords:
Pinus pinaster
Pinus pinea
Dendroclimatology
Climate change
Tree resilience

ABSTRACT

In Mediterranean forests, increasing tree susceptibility to drought has often been attributed to local site conditions and species-specific adaptations to water scarcity. Climate-growth relationship has been assumed to be stationary; however, warming can induce non-stationary relationships. This study aimed to evaluate whether recent warming has induced non-stationary growth responses in Mediterranean forests. For these two Mediterranean pine species with different life-history traits (*Pinus pinea* and *Pinus pinaster*), were studied using dendrochronological data, in two areas of Portugal with distinct Mediterranean Type climate (Csb - warm-summer Mediterranean, and Csa - hot-summer Mediterranean). We evaluated average tree ring indices for two periods, before and after the 1970s onset of the warming trend, to determine potential changes in growth sensitivity to moisture availability. Our results reveal that increased warming after the 1970s induced contrasting species-specific responses. Fast growing *P. pinaster* had enhanced growth during favorable conditions at mesic sites. In contrast, the more xeric *P. pinea* reduced growth under warming, indicating a change in consideration of these two species capacities to cope with future climatic conditions. We have not found an increase in sensitivity to water availability during warming, therefore, future drought recovery for both species will largely depend on local declines in water availability. These findings highlight the importance of accounting for non-stationary climate–growth relationships when predicting species responses to climate change. Understanding the mechanisms driving tree resilience is critical for developing more accurate and effective forest management strategies under future scenarios of warming and more frequent and severe droughts.

1. Introduction

In recent decades, global environmental changes have intensified at an unprecedented rate, with rising temperatures outpacing increases in precipitation, contributing to a higher frequency and severity of extreme climatic events such as droughts (Bednar-Friedl et al., 2022; Vicente-Serrano et al., 2014). Forest ecosystems are particularly vulnerable to these changes, as more intense and frequent droughts can limit tree growth (Campôa et al., 2021; Campôa and Puhlick, 2023; Sánchez-Salguero et al., 2010), increase tree mortality rates (Allen et al., 2010; Dale et al., 2001; McDowell et al., 2008), and enhance trees susceptibility to pests and pathogens (Ayres and Lombardero, 2000; Dale et al., 2001; Millar and Stephenson, 2015). Drought and associated stressors may lead to substantial shifts in species composition altering successional trajectories (Allen et al., 2010; Clark et al., 2016; Millar and Stephenson, 2015), and impair the capacity of forests to provide essential ecosystem services such as carbon storage (Allen et al., 2010; Case et al., 2021; Millar and Stephenson, 2015).

Understanding how trees respond to drought under changing climatic conditions is essential for predicting future forest stand dynamics and informing land management and conservation strategies (Dale et al., 2001; Millar and Stephenson, 2015; Nocentini et al., 2017). A reliable proxy for evaluating trees responses to climatic stressor, such as droughts, has been the analysis of long-term radial growth (DeSoto et al., 2020; Lloret et al., 2011; Nikinmaa et al., 2020). Accordingly with the dendrochronological principle of uniformitarianism, the relationship between climate and growth is assumed to remain stable over time (Fritts, 1976). It is based on this assumption that dendroclimatic models

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https://doi.org/10.1016/j.dendro.2026.126469
Received 16 September 2025; Received in revised form 23 December 2025; Accepted 3 January 2026
Available online 5 January 2026

have been used to reconstruct past climate and to identify tree climatic drivers of growth (Luckman, 2013; Sheppard, 2010). However, recent evidences have been challenging this view, considering that tree climate-growth relationships and climate sensitivity may be non-stationary (Wilmking et al., 2020).

Considering the non-stationarity of climate–growth relationships, novel associations and heightened climate sensitivity may emerge (Camarero et al., 2021; Campôa and Puhlick, 2023; Diers et al., 2024; Leifsson et al., 2024; Natalini et al., 2015; Zampieri et al., 2024), thereby altering our considerations of species' drought susceptibility (Campôa and Puhlick, 2023). Non-stationarity can be driven by parameters such as increasing temperatures (Babst et al., 2019; Leifsson et al., 2024), yet these changes are not uniform and depend on species- and site-specific traits, reflecting the plasticity of trees in responding to local environmental conditions (Leifsson et al., 2024; Tumajer et al., 2023).

Studies have shown that trees may become more susceptible to increasingly frequent and intense drought events (Gazol et al., 2016; Liu et al., 2025; Serra-Maluquer et al., 2018; Veuillen et al., 2023). This increased susceptibility has often been attributed to decreased local water availability, which limits trees capacity to grow during dry periods (Bose et al., 2020; Sánchez-Salguero et al., 2018; Vergarechea et al., 2021; Zang et al., 2014; Zhang et al., 2021). However, under the hypothesis of non-stationarity, reduced growth during prolonged and more intense droughts may not only reflect changes in water availability, as expected under a stationary framework, but also arise from novel climatic drivers of growth or increased climate sensitivity. In this latter case, trees may perform even more poorly under prolonged and more intense droughts (Leifsson et al., 2024; Natalini et al., 2015), highlighting the importance of clarifying whether species exhibit stationary or non-stationary climate–growth relationships. This distinction is critical, as trees with reduced capacity to grow and recover after drought are at greater risk of drought-induced mortality (DeSoto et al., 2020), yet most studies do not explicitly evaluated non-stationary responses (Wilmking et al., 2020).

The Mediterranean climate is characterized by mild, wet winters and hot, dry summers, and the region prone to recurrent anomalous drought events (Bednar-Friedl et al., 2022; Cook et al., 2016). In this environment, water availability is the primary limiting factor for tree growth (Campôa et al., 2021; Sarris et al., 2013), so growth is reduced during droughts (Gazol et al., 2017; Sánchez-Salguero et al., 2010; Serra-Maluquer et al., 2018). A reduction in local water availability has been commonly used to explain increased drought susceptibility in studies conducted in Mediterranean forests (Sánchez-Salguero et al., 2018; Vergarechea et al., 2021; Veuillen et al., 2023). However, since the 1970s the region has experienced a pronounced warming trend, leading to an increase in both the frequency and intensity of drought events in recent decades (Cook et al., 2016; Hertig & Tramblay, 2017; Vicente-Serrano et al., 2014). Yet it remains unclear whether recent warming has altered the way Mediterranean trees respond to drought. Addressing this gap could provide a more accurate understanding of the capacity of Mediterranean trees to cope with these increasing climatic disturbances.

To study if the warming trend after the 1970's is leading to changes in climate-growth relationships and increased sensitivity to moisture availability, the present work investigates the response of trees to drought at northern and southern sites in Portugal, a country situated in the western Mediterranean basin that has experienced a significant warming trend since the 1970s (Espírito Santo et al., 2014). The climate in Portugal follows a marked latitudinal gradient, largely due to topographic variation. Areas north of the Tagus River are generally wetter and predominantly classified as Csb (warm-summer Mediterranean climate) under the Köppen classification, while southern regions are drier and mainly fall under the Csa type (hot-summer Mediterranean) (Mora and Vieira, 2020; Santos et al., 2019).

Because of the wide distribution and ecological importance of pines in Mediterranean forests (Tapias et al., 2004; Torres et al., 2021), two different pine species were selected for this study, *Pinus pinaster* and *Pinus pinea*. Although these species often coexist, they differ in their life history traits and drought response strategies. *Pinus pinaster* is a relatively fast-growing species that adopts an isohydric water-use strategy, which involves closing stomata rapidly under water stress to minimize water loss (Férriz et al., 2023; Ledo et al., 2014). While this strategy helps prevent hydraulic failure, it also reduces carbon assimilation and can limit growth during drought conditions (McDowell et al., 2008). In contrast, *P. pinea* grows more slowly and follows a more anisohydric response, maintaining stomatal conductance and physiological activity even during periods of low water availability (Férriz et al., 2023; Ripullone et al., 2007). This behavior supports continued growth under drought (McDowell et al., 2008) and reflects an adaptation to water stress.

Non-stationary responses vary with species- and site-specific traits, reflecting the plasticity of trees to local environmental condition (Leifsson et al., 2024; Tumajer et al., 2023). Therefore, in this study we take advantage of the contrasting life-traits traits of two abundant pine species (*P. pinea* and *P. pinaster*) together with their exposure to the distinct temperature and precipitation regimes occurring in Portugal, to assess how these factors shape their drought responses across Mediterranean biogeographic regions under climate change. This research aims to bridge the gap between species-specific ecological traits, biogeographic context, and long-term novel climatic trends to improve our understanding of how observed warming has affected tree sensitivity to drought in the Mediterranean. For this we used dendrochronological techniques, which allow for the analysis of long-term growth patterns in response to climatic variables (Fritts, 1976) and the detection of temporal shifts in climate–growth relationships (Campôa and Puhlick, 2023; Natalini et al., 2015; Zampieri et al., 2024). We hypothesize that due to recent warming, Mediterranean pines follow non-stationary behavior and become more sensitive to moisture variability. The outcomes of this study will enhance the capacity to predict forest stand dynamics under future climatic conditions and support the development of adaptive strategies that promote forest resilience in drought-sensitive environments.

2. Material and methods

2.1. Study sites

To capture the climatic differences in Portugal and assess tree responses to drought across different Mediterranean conditions, two study sites were selected, one north and one south of the Tagus River, representing wetter and drier Mediterranean climates respectively (Fig. 1). Both sites are managed by the national forest authority, ICNF (Instituto da Conservação da Natureza e das Florestas), and were chosen because they support the coexistence of *P. pinaster* and *P. pinea.*

At the northern site, where *P. pinaster* is the dominant species, trees were sampled at the Leiria National Forest (11,000 ha), an area for optimal growth for this species. In a nearby forest, *P. pinea* was sampled in the Valado National Forest (1400 ha), located about 20 km from Leiria National Forest. At the southern site, where *P. pinea* predominates, sampling was carried out in optimal growth areas for this species. *Pinus pinea* and *P. pinaster* trees were sampled in the Sines Forest Perimeter (9500 ha). Older *P. pinea* trees were also sampled in the neighboring Valverde National Forest (952 ha), situated roughly 40 km from Sines.

2.2. Climatic data

Long-term monthly data (1901 onwards) on temperature, precipitation, and drought indices were obtained from the Climate Research Unit Time-Series version 4.08 dataset. Temperature and precipitation data were accessed through the Google Earth Interface (https://crudata.uea.ac.uk/cru/data/hrg/; Harris et al., 2020) while drought indices

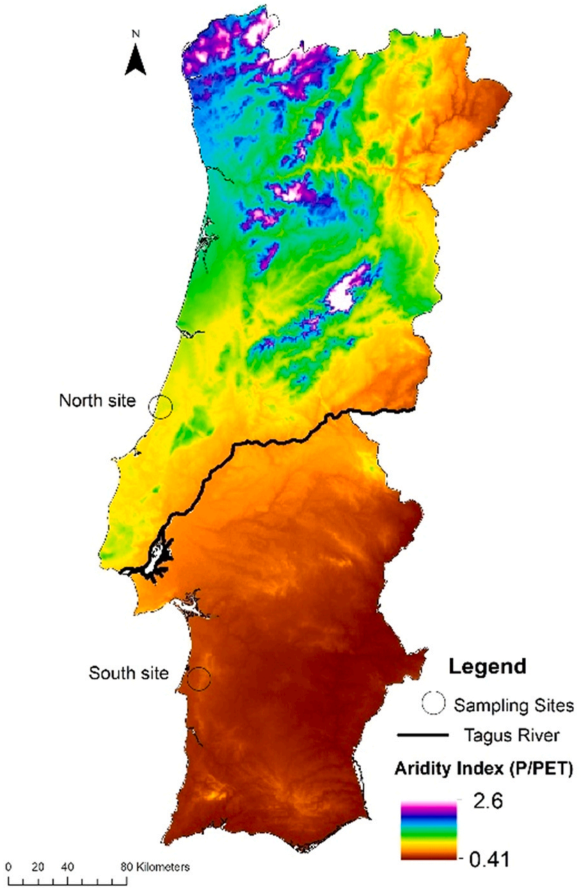

Fig. 1. Location of the study sites and the spatial distribution of the aridity index (Precipitation (P) to Potential Evapotranspiration (PET) in Portugal. Data retrieved from the CGIAR Consortium for Spatial Information: https://csidotinfo.wordpress.com/). Lower aridity index values indicate dry conditions while greater values indicate wetter conditions.

were retrieved via the KNMI Climate Explorer platform (https://climexp.knmi.nl/start.cgi; van der Schrier et al., 2013). We used the self-calibrating Palmer Drought Severity Index (scPDSI), a normalized drought index that adjusts to local climatic baselines by calibrating its water balance model to historical site-specific conditions. The scPDSI integrates precipitation, temperature, and soil moisture data to quantify drought severity over time, adjusting for regional hydroclimatic variability, better identifying extreme wet and dry local conditions. Positive values indicate wetter conditions, whereas negative values reflect increasing moisture deficits (Wells et al., 2004).

Two periods were defined to assess temporal shifts in climate: Period 1 (1901–1969), representing the interval before the onset of the warming trend, and Period 2 (1970–2021), corresponding to the period influenced by ongoing warming (Espírito Santo et al., 2014). To test for significant differences in climatic conditions between periods and between study sites (North and South), linear models of temperature and precipitation were developed using annual data. Site, period, and their interaction were considered for inclusion in the models as explanatory variables. We followed a stepwise approach: the interaction term was tested first, and if not significant, it was removed. Then, the reduced model with the main effects was evaluated. Finally, non-significant main effects were removed, one by one, to yield an optimal model in terms of explanatory variables. Because scPDSI is normalized to each site's local climatic baseline, direct comparisons between sites could be misleading. Therefore, we developed separate linear models for each site, using Period as the explanatory variable.

Next, to evaluate the temporal variation in climate conditions, annual anomalies were calculated for each climatic variable as deviations from the reference mean. The reference mean was defined as the average for the period 1970–2021, corresponding to the onset of the observed warming trend in Portugal. To assess long-term trends, a linear regression was fitted to the anomaly time series for each variable.

2.3. *Obtaining dendrochronological series*

To obtain dendrochronological data, increment cores were extracted from healthy, dominant or codominant trees using a 0.5-centimeter diameter increment borer (Haglöf Sweden®). Most of the sampling was conducted in 2022, although cores had already been obtained in 2016 from *P. pinaster* trees at the northern site. At this site, we also obtained cross sections from 19 *P. pinaster* trees. The increment cores and cross sections were collected at breast height (1.30 m). Cores were dried and mounted on wooden supports. Cross sections were also dried and sectioned into thin longitudinal strips through the pith to facilitate processing. All samples were sanded to enhance tree ring visibility and scanned. For each tree cored in 2022, total tree height was measured using a Vertex 5 (Haglöf Sweden®), diameter at breast height was measured using a caliper, and basal area was measured using a wedge prism with a basal area factor of 10, following protocol by Calvão et al. (2019).

Tree ring widths were measured and dated using the CooRecorder and CDendro software version 9.6. Cross dating accuracy was verified using COFECHA (Holmes, 1983), and only trees with a minimum correlation of 0.3 with our master chronology were retained (Nabais et al., 2014). This subset of trees had a mean (± SD) growth series intercorrelation of 0.64 ± 0.10 and 0.59 ± 0.09 for *P. pinaster* in the north and south, respectively, and 0.58 ± 0.06 and 0.60 ± 0.10 for *P. pinea* in the north and south, respectively. The influence of age-related growth-trends were removed using the R package detrendeR (Campelo et al., 2012). To obtain the detrended tree-ring indices (TRI), the ring width series using a spline with a 50 % frequency cutoff and a length of 67 % of the mean series length, as recommended by Klesse (2021). Then, a biweight robust mean was computed using the detrended TRI series to obtain detrended chronologies for each species at each study site. We did not apply an autoregressive model, because we wanted to examine potential lag effects in tree growth (Bose et al., 2021; Peña-Gallardo et al., 2018). By preserving this temporal signal, the biogeographic influences of drought on tree growth responses to drought can be evaluated.

2.4. *Stationarity of climate-growth relationships*

To evaluate whether climate–growth relationships remained stationary over time or shifted under changing climatic conditions, we applied the dcc function from the R package treeclim (Zang and Biondi, 2015). A moving correlation analysis was performed using a 30-year sliding window between the detrended chronologies and climate variables. We used a 30-year window because it corresponds to the standard length for defining climatic normals. Since climatic conditions from the previous year can influence tree growth (Caminero et al., 2018; Campôa et al., 2021; Nabais et al., 2014), we performed this analysis from September of the year before growth to October of the current growth year.

2.5. *Tree growth and drought sensitivity between periods*

To evaluate changes in tree growth over time and between regions, we calculated the mean TRI for each tree during two temporal periods. These periods were defined to capture growth patterns before and after the onset of recent climate warming (Espírito Santo et al., 2014). To select a robust starting year for Period 1, we calculated the Subsample Signal Strength (SSS), which quantifies how well a subset of tree-ring series represents the full population signal. SSS is particularly useful for identifying the point where chronologies become reliable when early portions of the series have low replication (Buras, 2017; Cook and Kairiukstis, 1992). Period 1 was therefore defined from the first year in which all chronologies' SSS reached 0.85 until 1969. Period 2 extended from 1970 to 2015 for *P. pinaster* and to 2021 for *P. pinea*. We allowed different end years to retain the maximum possible information for each species. For *P. pinea* in the northern site, only Period 2 was considered in subsequent analyses because the number of years before 1970 was extremely limited. For the full period covered by each chronology (Period 1 + Period 2), we also calculated the Expressed Population Signal (EPS), which evaluates the strength of the common growth signal among trees. Consistent with standard dendrochronological criteria, EPS values ≥ 0.85 were considered indicative of adequate chronology quality (Buras, 2017; Cook and Kairiukstis, 1992). The SSS and EPS indices were obtained using the R package dplR (Bunn, 2008).

The TRI is a standardized measure that reflects relative rather than absolute growth, allowing for comparisons of tree growth response to climate between time periods (Fritts, 1976). To assess the effect of site and period on changes in the mean TRI, we evaluated linear models for each species. For *P. pinaster*, explanatory variables included site, period, and their interaction. For *P. pinea*, to test the effect of site, we only considered the data from Period 2. To test the effect of period, we only considered data from *P. pinea* in the south. To further assess tree responses to moisture variability and to determine whether these relationships differed between periods, we evaluated linear models with annual TRI as the response and scPDSI, period, and their interaction as predictors for *P. pinaster* and for *P. pinea* at the southern site. For *P. pinea* in the north, we evaluated a linear model with only scPDSI as an explanatory variable. To obtain the optimal models we used the stepwise approach as explained earlier

In all developed models, variance inflation factors were checked to ensure the absence of collinearity among predictors. Mean values were estimated as least-square means using the emmeans package. All analysis were performed using R version 4.4.2.

3. Results

3.1. Climate

Both sites exhibited a significant increase in temperature anomalies over time (Fig. 2A and B), with lower values recorded during the first period (1901–1969) compared to the second period (1970–2021; Table 2). In the most recent period, mean annual temperature reached 16.8 ± 0.06 °C in the north and 17.3 ± 0.06 °C in the south (Fig. 3A). In contrast, we did not detect a significant linear trend in precipitation anomalies over time (Fig. 2C and D). However, regional differences persisted across both periods with the northern site receiving greater annual precipitation than the south (Fig. 3B). From 1970–2021, annual precipitation was 789 ± 18.9 mm (mean ± SE) in the north compared to 615 ± 18.9 mm in the south. The drought index (scPDSI) declined significantly over time at both sites (Fig. 2E and F), indicating increasingly drier conditions across the study area between periods (Table 2). In the north, scPDSI index reduced from 0.266 ± 0.200 to −0.557 ± 0.230, and in the south, from 0.469 ± 0.223 to −0.596 ± 0.256.

3.2. Stationarity of climate-growth relationships

Overall, temperature–growth relationships were non-stationary. For trees in the south, correlations became more pronounced in recent years,

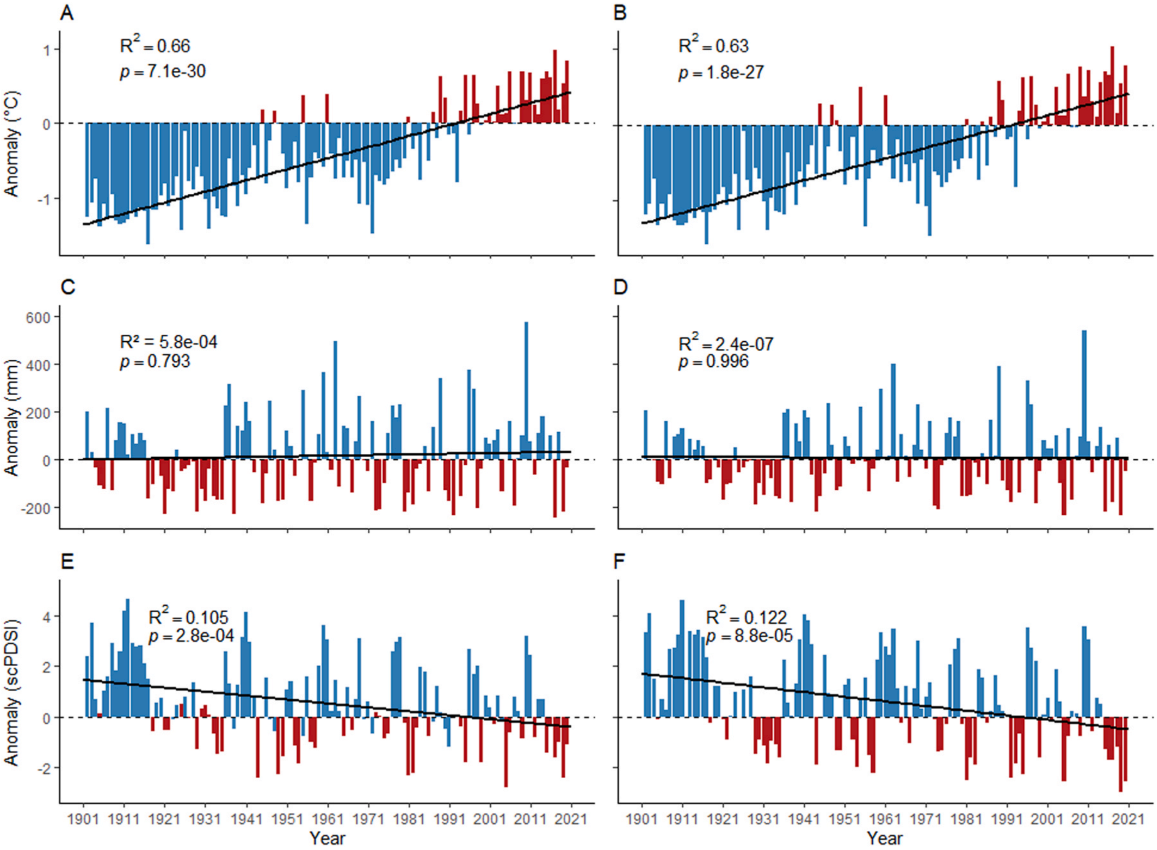

Fig. 2. Annual anomalies in mean annual temperature (°C), total precipitation (mm), and drought (scPDSI) for the North (A, C, E) and South (B, D, F) sites from 1901 to 2021. Anomalies were calculated relative to the 1970–2021 baseline mean. Red bars indicate conditions above normal (hotter) for temperature (A, B) and below normal (drier) for precipitation and scPDSI (C–F). Blue bars indicate cooler or wetter than normal years. Solid black lines represent linear trends, and corresponding R^2 and p-values are shown in each panel.

Table 1

Sites characterization and dendrometric attributes of the sampled sites. Geographic coordinates (Lat - latitude and Long - longitude), tree species sampled, number of sampled trees (N), span of the tree-ring chronology, mean height (H, m), mean diameter at breast height (DBH, cm) and mean basal area (m^2/ha) reported separately for conspecific pines (BASP), other pine species (BAOP), and non-pine species (BANP). Standard errors in parentheses. Dendrometric values are not available for the sampled P. pinaster in the North site due to different sampling acquisition.

	Lat	Long	Species	N	Span	H	DBH	BA_{SP}	BA_{OP}	BA_{NP}
North	39.69	-9.02	*P. pinaster*	23	1938–2015	-	-	-	-	-
			P. pinea	8	1960–2021	14.1 ± 0.45	41.29 ± 1.81	22.24 ± 1.95	1.15 ± 0.61	-
South	38.03	-8.70	*P. pinaster*	14	1950–2021	20.39 ± 0.55	42.68 ± 0.70	4.90 ± 1.30	3.00 ± 1.00	0.40 ± 0.30
			P. pinea	25	1830–2021	18.10 ± 0.56	54.46 ± 2.80	8.31 ± 1.05	0.83 ± 0.39	0.25 ± 0.19

Table 2

Results of the linear model testing the effects of Site (North and South), Period (Period 1 and Period 2), and their interaction on mean annual temperature, total annual precipitation, and annual mean scPDSI. Period 1 ranges from 1901 to 1969, and Period 2 ranges from 1970 to 2021. For scPDSI, the effect of Period for sites was tested individually. DF – degrees of freedom; SS – sum of squares; MS – mean squares; F – F-values; P – p-value.

			DF	SS	MS	F	P
Temperature	Site		1	20.291	20.291	81.032	< 0.001
	Period		1	37.743	37.743	150.724	< 0.001
	Residuals		239	59.849	0.250		
Precipitation	Site		1	1817501	1817501	70.574	< 0.001
	Residuals		240	6180741	25753		
scPDSI	North	Period	1	20.090	20.093	7.289	0.008
		Residuals	119	328.030	2.757		
	South	Period	1	33.680	33.677	9.855	0.002
		Residuals	119	406.660	3.417		

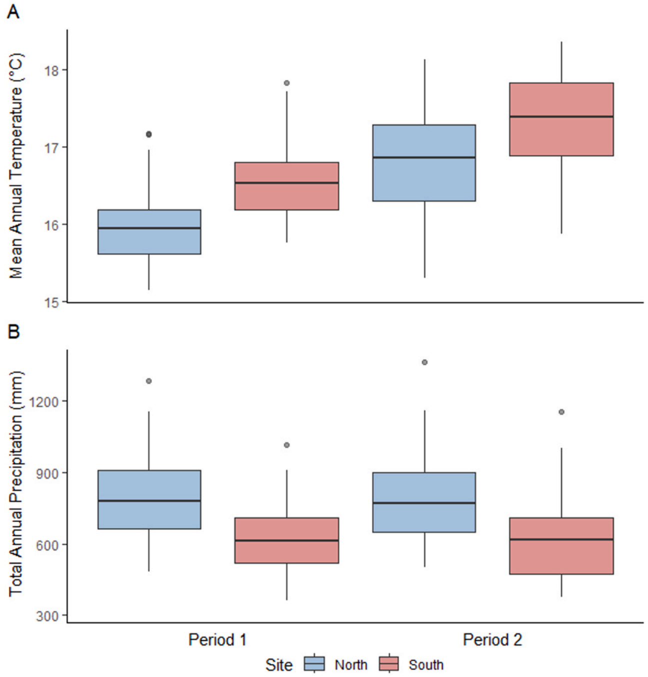

Fig. 3. Distribution of mean annual temperature (A) and total annual precipitation (B) for the North and South sites in the two time periods. Period 1 ranges from 1901 to 1969, and Period 2 ranges from 1970 to 2021.Dots outside the plot's whiskers represent outliers.

with both species showing negative correlation with July temperatures and *P. pinea* showing more consistent positive correlation with January temperatures (Fig. 4). In the north, *P. pinaster* exhibited a significant negative correlation with growing-season temperatures during the early period, in particular during March and June, which become non-significant after the 1970s.

After the 1970's, in the north, both *P. pinaster* and *P. pinea* developed positive correlations with February precipitation, a pattern not observed in earlier decades and *P. pinaster* showed a consistent positive correlation with January precipitation (Fig. 5). A similar temporal shift was seen in the drought–growth relationship (Fig. 6), where *P. pinaster* shifted from responding to summer months scPDSI (May to August) in the earlier period to showing positive correlations with scPDSI, from January to April, after the 1970s.

In the south, both species exhibited positive correlation with previous December and January precipitation, and *P. pinea* also exhibited a relatively constant positive correlation with February precipitation (Fig. 5). Both *P. pinaster* and *P. pinea* showed positive correlation with scPDSI across all months in the more recent decades (Fig. 6). For *P. pinea*, this year-round sensitivity to moisture has been more stationary over time, from previous December to current October. *Pinus pinaster*, on the other hand, initially appeared to respond mainly to moisture from June to August, but became more dependent on moisture conditions from previous December to current October in recent decades.

3.3. *Tree growth and drought sensitivity between periods*

The starting year for Period 1 was set at 1955, corresponding to the first year in which the SSS exceeded the threshold of 0.85 in all chronologies (Fig. 7), with exception to *P. pinea* in the north that is not considered for Period 1. Period 1 therefore spans 1955–1969. Period 2 was defined from 1970 to 2015 for *P. pinaster* and from 1970 to 2021 for *P. pinea*. Across the full study period (Periods 1 and 2 combined), the EPS exceeded the minimum threshold of 0.85 for all chronologies (Table 3).

For *P. pinaster*, mean TRI increased ($p = 0.012$; Table 4) from 0.972 ± 0.018 (mean ± SE; Period 1) to 1.015 ± 0.017 (Period 2). However, the increase was not the same in the two sites (interaction effect: $p < 0.05$; Table 4), with an increase in TRI being clearer in the north (Fig. 8). Differently, for *P. pinea* in the south (Fig. 9), the model indicates a reduction in the mean TRI between periods, with mean TRI being higher in the first period (1.068 ± 0.016) than in the second period (0.985 ± 0.016; $p < 0.001$; Table 4). During Period 2, no difference between sites was detected.

For both species, tree growth responded positively to scPDSI, indicating that lower scPDSI (drier conditions) leads to lower growth (*P. pinaster*: coefficient = 0.050, $t = 11.719$, $p < 0.001$; *P. pinea* North: coefficient = 0.028, $t = 2.877$, $p = 0.004$; *P. pinea* South: coefficient = 0.080, $t = 16.25$, $p < 0.001$;Table 5). No significant interaction was

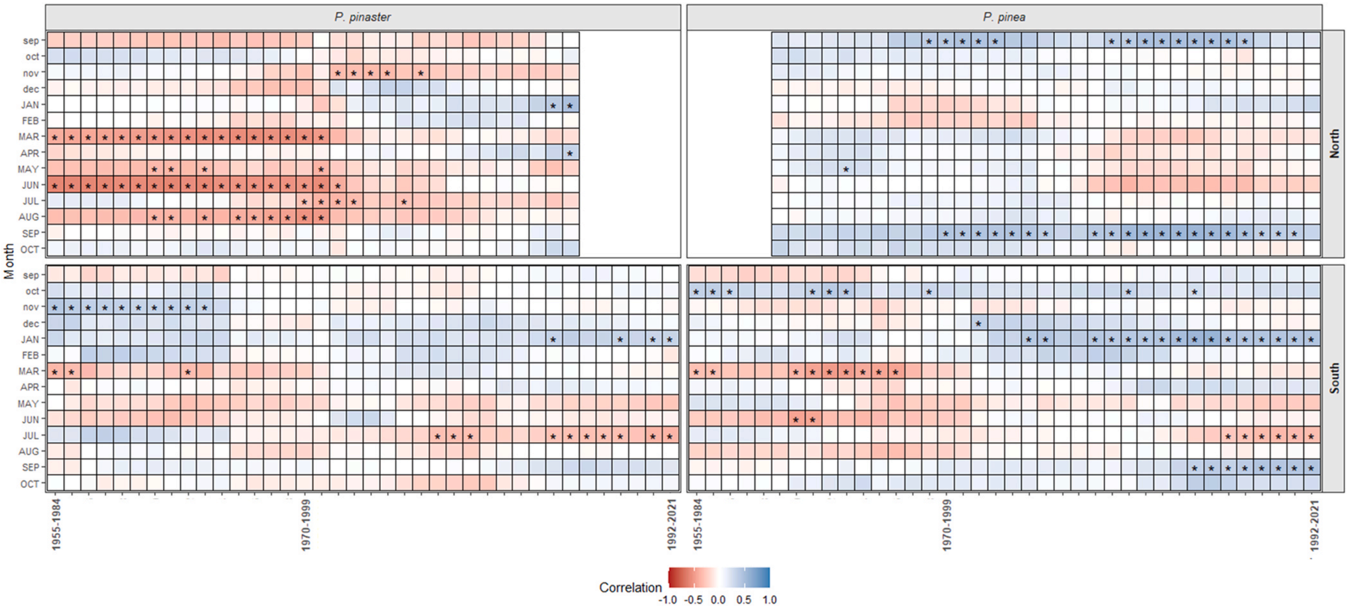

Fig. 4. Correlation coefficients from a 30-year moving window correlation analysis between monthly mean temperature and site chronologies for each species, from 1955-1984 to 1992–2021. Lowercase months indicate months prior to the growth year, while uppercase months denote months within the current growth year. An asterisk (*) marks correlations that are statistically significant ($p < 0.05$). The figure with full temporal window is provided in Supplementary Fig. S1.

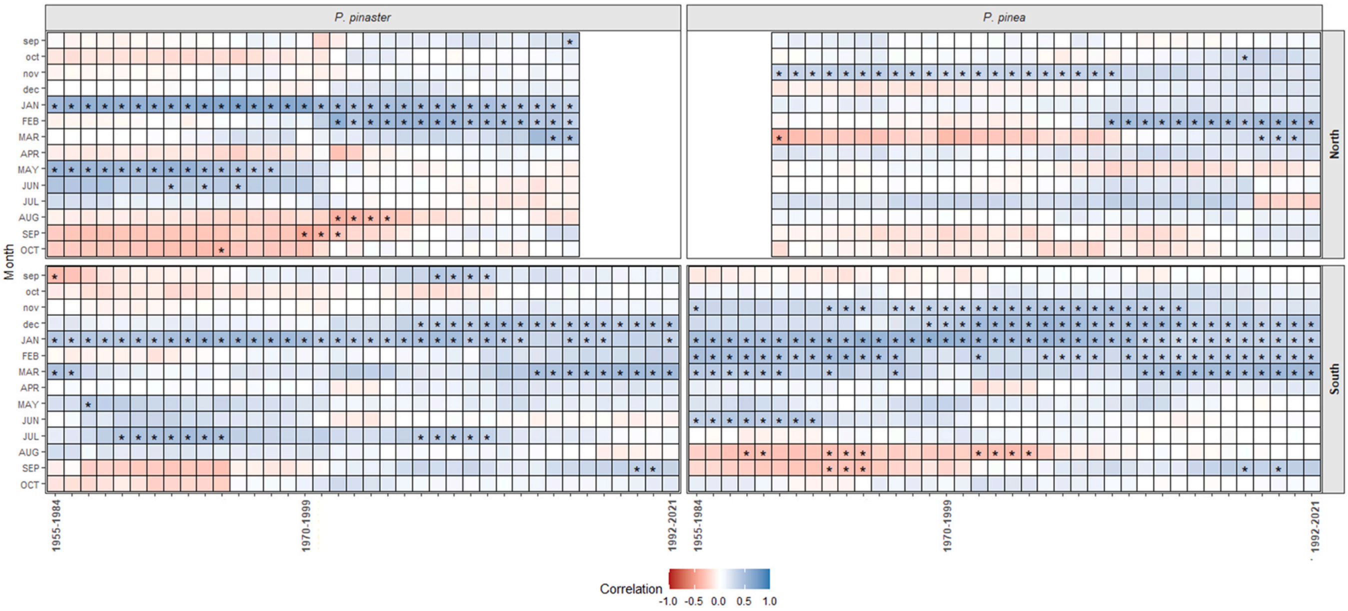

Fig. 5. Correlation coefficients from a 30-year moving window correlation analysis between total monthly precipitation and site chronologies for each species, from 1955-1984 to 1992–2021. Lowercase months indicate months prior to the growth year, while uppercase months denote months within the current growth year. An asterisk (*) marks correlations that are statistically significant ($p < 0.05$). The figure with full temporal window is provided in Supplementary Fig. S2.

found for *P. pinaster* and *P. pinea* in the south, indicating similar drought sensitivity between period.

4. Discussion

4.1. Climatic evolution and differences between sites

In the present work, we studied how warming trend differentially affected the growth of two co-occurring pine species, a fast-growing species, *Pinus pinaster*, and a xeric-adapted species, *Pinus pinea*, across two Portuguese coastal forests that represent distinct Mediterranean biogeographical contexts: warm-summer Mediterranean and hot-summer Mediterranean. In both sites, a significant warming trend occurred as expected, particularly after the 1970s. Although temperatures increased similarly in the two biogeographic regions, this trend was not accompanied by corresponding increases in precipitation. This resulted in progressively drier conditions over time due to higher evapotranspiration, reflecting the broader global trend in which drying conditions are driven by increasing temperatures (Bednar-Friedl et al., 2022; Vicente-Serrano et al., 2014). The climatic contrast between the two sites was consistent with the expected climatic gradient. While both fall within the Mediterranean climate zone, the northern site is characterized by lower temperatures and higher precipitation, whereas the southern site experiences hotter and drier conditions, indicative of a

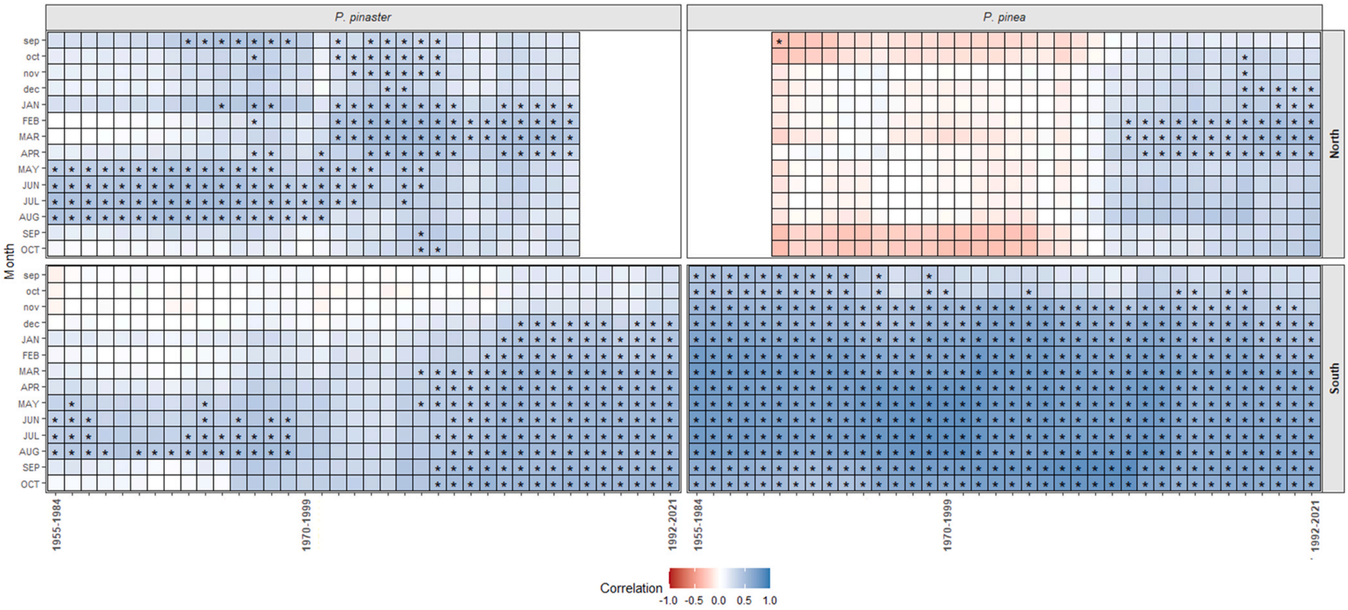

Fig. 6. Correlation coefficients from a 30-year moving window correlation analysis between monthly scPDSI and site chronologies for each species, from 1955-1984 to 1992–2021. Lowercase months indicate months prior to the growth year, while uppercase months denote months within the current growth year. An asterisk (*) marks correlations that are statistically significant ($p < 0.05$). The figure with full temporal window is provided in Supplementary Fig. S3.

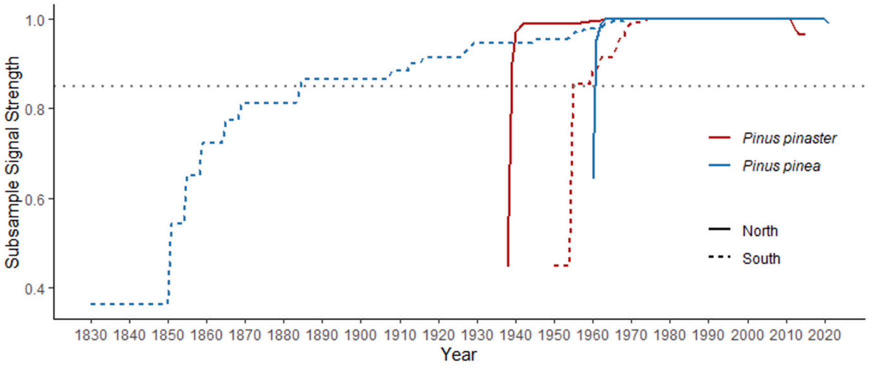

Fig. 7. Subsample Signal Strength (SSS) over time for both species in the two sites. Dotted grey line identifies SSS = 0.85.

Table 3
Expressed Population Signal (EPS) for both species in the two sites. For P. pinaster the common period of 1955–2015 was used. For P. pinea in the north, the period was 1970–2021, and in the south, the period was 1955–2021.

	North	South
Pinus pinaster	0.948	0.905
Pinus pinea	0.928	0.929

more arid Mediterranean climate, suggesting a greater drought stress (Mora and Vieira, 2020; Santos et al., 2019).

4.2. Non-stationarity of climate-growth relationships

In the drought-prone Mediterranean, it is crucial to understand how trees respond to increasing water stress, as the stability of future forests will largely depend on the capacity of trees to cope with droughts. While reduced water availability has long been recognized as a driver of declining resilience under increasingly frequent and severe droughts, our study highlights that recent warming has also altered climate–-growth relationships. Notably, the shifts in climate–growth relationships observed in our study aligns with the onset of the increasing warming trend registered since the 1970’s (Figs. 4, 5 and 6).

Similar to the finding of Tumajer et al. (2023) in central and northern Europe, our results in the Mediterranean indicate that the nature and extent of these changes differed by species and site. *Pinus pinaster* exhibited greater non-stationarity in its climate response compared to *P. pinea*, particularly at the northern site. This is consistent with the ecological strategy of *P. pinaster*, which is often described as having high phenotypic plasticity (Bert et al., 2021; Toca et al., 2019; Vieira et al., 2019), allowing it to adjust more readily to changing environmental conditions in pursuit of fast growth and opportunistic behavior (Tapias et al., 2004; Viñas et al., 2016). At the site level, trees in the northern region displayed more pronounced shifts in their climate–growth relationships than those in the south. The northern site, being wetter and less environmentally limiting, may offer more favorable conditions for trees to modulate their physiological responses to climate (Corcuera et al., 2011; Toca et al., 2019; Tumajer et al., 2023). This finding aligns with previous studies showing that trees growing in mesic environments tend to exhibit greater plasticity and adaptability to changing climatic conditions compared to those in more constrained, drought-prone sites (Corcuera et al., 2011; Tumajer et al., 2023).

A study by Nabais et al. (2014), conducted with *P. pinaster* in northern Portugal and *P. pinea* in a southern Portugal, found that

Table 4
Results of linear models assessing the effect of site (North and South) and period (Period 1 and Period 2) on the mean TRI for P. pinaster and P. pinea. For each tree, the mean TRI was calculated separately for each period. Period 1 ranges from 1955 to 1969 for both species, whereas Period 2 ranges from 1970 to 2015 for P. pinaster and from 1970 to 2021 for P. pinea. For P. pinea, the model assessing the effect of Period only has data of the Southern site, and the model assessing the effect of Site, is only with data of Period 2. DF – degrees of freedom; SS – sum of squares; MS – mean squares; F – F-values; P – p-value.

			DF	SS	MS	F	P
P. pinaster	Site		1	0.026	0.026	2.713	0.104
	Period		1	0.064	0.064	6.628	0.012
	Site*Period		1	0.060	0.060	6.227	0.015
	Residuals		68	0.659	0.010		
P. pinea	South	Period	1	0.085	0.085	12.851	< 0.001
		Residuals	48	0.319	0.007		
	Period 2	Site	1	5×10^{-6}	4.56×10^{-6}	0.003	0.959
		Residuals	31	0.053	0.002		

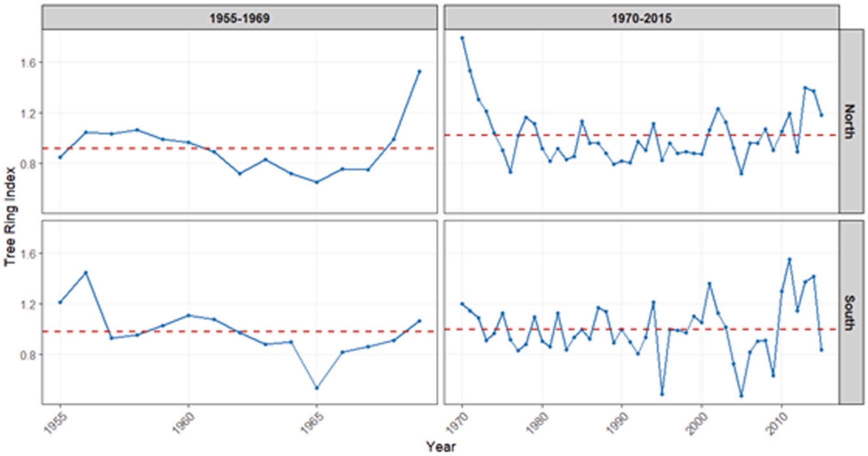

Fig. 8. Detrended chronologies for Pinus pinaster for the two periods at both sites. Red dashed line indicates the mean value of Tree Ring Index.

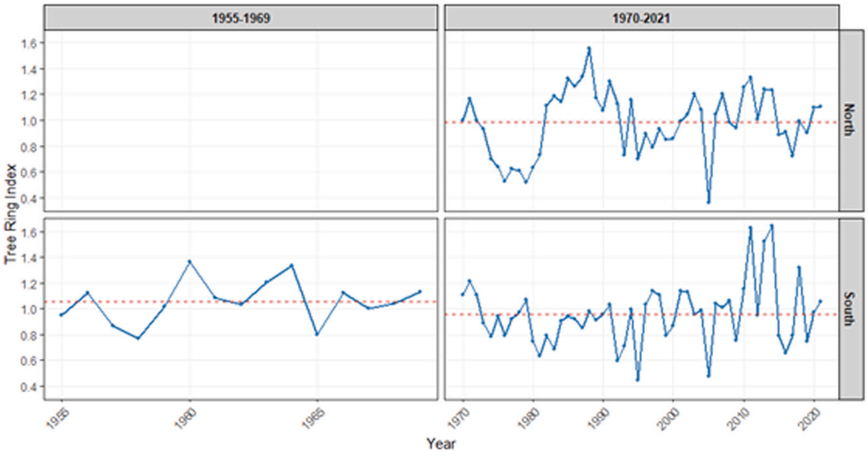

Fig. 9. Detrended chronologies for Pinus pinea for the two periods at both sites. Red dashed line indicates the mean value of Tree Ring Index.

Table 5
Results of linear models assessing the effects of drought (scPDSI) and period (Period 1 VS Period 2) on annual TRI for P. pinaster and P. pinea. Period 1, which includes TRI values up to 1969, and Period 2, includes TRI values from 1970 onwards. DF – degrees of freedom; SS – sum of squares; MS – mean squares; F – F-values; P – p-value.

			DF	SS	MS	F	P
P. pinaster	scPDSI		1	10.618	10.618	109.968	< 0.001
	Period		1	5.169	5.1690	53.535	< 0.001
	Residuals		2093	202.087	0.097		
P. pinea	North	scPDSI	1	0.775	0.775	8.276	0.004
		Residuals	413	38.673	0.094		
	South	scPDSI	1	32.261	32.261	264.23	< 0.001
		Residuals	1609	196.451	0.122		

P. pinaster growth was negatively correlated with late spring and summer temperatures, while both species showed positive correlations with winter and early spring precipitation. Our results are generally consistent with these patterns. However, following the shift in climate–growth relationships identified around the 1970s, *P. pinaster* in the north no longer exhibited a strong negative correlation with growing season temperatures (March and June). Instead, both pine species have become more responsive to water-related variables (i.e., precipitation and drought) at both of our study sites. This increasing dependence on water availability and less limitation by temperature has also been noted in recent literature evaluating forest responses to warming conditions (Camarero et al., 2021; Natalini et al., 2015). While temperature remains important for initiating cambial activity (Buttò et al., 2025; Vieira et al., 2014), water availability may have become the main climatic driver, as it directly influences the xylogenesis process (Buttò et al., 2025; Vieira et al., 2014, 2015, 2020). Under the current climatic regime, our results and those of others support those findings and suggest that precipitation preceding the onset of the growing season and sustained moisture availability throughout the year are the primary climatic drivers of radial growth (Babst et al., 2019; Camarero et al., 2021; Férriz et al., 2021; Natalini et al., 2015).

We recognize that the use of moving correlations involves a large number of overlapping windows, which increases the likelihood of Type I errors. However, because successive 30-year windows are highly autocorrelated, applying strict corrections such as the Bonferroni adjustment would substantially inflate the risk of Type II errors (Doan, 2005), potentially masking true climate–growth relationships. For this reason, we opted not to apply multiplicity corrections, recognizing this as a limitation of our approach. To minimize the risk of over-interpreting spurious correlations, we focused our interpretation only on consistent patterns of significance that persisted across multiple consecutive windows rather than isolated significant values. Readers should therefore interpret our moving-correlation results with this consideration in mind.

4.3. Tree growth and drought response under warming

Both species responded positively to scPDSI, indicating that growth increases under moist conditions and is reduced during drier years. Contrary to our initial expectations, drought sensitivity did not differ markedly between periods, suggesting that non-stationarity did not increase growth sensitivity to moisture availability. Nevertheless, while *P. pinaster* showed mean TRI > 1, *P. pinea* showed mean TRI < 1 during the recent, warmer period (Table 4, Fig. 8 and 9). This suggests that the two species responded differently to warming: *P. pinaster* maintained or increased its growth potential, whereas *P. pinea* exhibited a reduction in growth, indicating a possible sensitivity to warming-induced water stress. Surprisingly, this pattern contrasts with the common assumption that *P. pinea* is the more drought-resilient species than *P. pinaster* (Férriz et al., 2023), as it is better adapted to proliferate in dry regions, like the south of Portugal.

In our study, Period 1 was shorter than Period 2, which may be considered a limitation because the unequal sample size reduces the amount of data available to characterize climate variability prior to the onset of recent warming. A smaller sample size in Period 1 also might reduce ability to detect climate–growth responses comparable to those observed in Period 2. However, it is important to note that the strongest climatic variability, particularly the more frequent and intense drought events, occurred predominantly during Period 2 (Agência Portuguesa do Ambiente, 2024). As such, most of the drought-related signal relevant to our hypotheses is concentrated in this later period.

Despite the drier conditions in the second period, notably, *P. pinaster* growth performance was particularly enhanced in the northern site. This pattern is likely linked to a shift in climate–growth relationships, whereby *P. pinaster* trees in the north became more dependent on precipitation and moisture availability during late winter to early spring (January to April; Figs. 5 and 6). This time of the year aligns with the peak of photosynthetic activity in Mediterranean pines (Maseyk et al., 2008) suggesting that trees in the north are now benefiting from water availability precisely when metabolic activity is highest, potentially enhancing carbon assimilation and metabolite production. *Pinus pinaster* in the southern site is more dependent on water availability throughout the year (Fig. 6) than in the north. In this generally drier environment, sustained moisture is less predictable and likely limits growth responses.

Water availability strongly regulates the xylogenesis process and growth cessation in Mediterranean pines (Vieira et al., 2014), where growth is constrained by the pronounced summer drought. As a result, these species typically adopt a bimodal growth pattern, with a major peak in spring and a secondary peak in autumn, allowing trees to capitalize on moisture availability before and after the dry season (Camarero et al., 2010; Campelo et al., 2021; Pacheco et al., 2018; Valeriano et al., 2023). This capacity for flexible cambial dynamics is further reflected in the formation of intra-annual density fluctuations (IADFs) in latewood cells, which signal intra-seasonal growth adjustments triggered by precipitation later in the growing period (Campelo et al., 2021; Nabais et al., 2014; Pacheco et al., 2018). Considering this adaptive capacity, and recent climate-growth relationships of *P. pinaster*, the enhanced growth response at the northern site align with the known response of the species, in which favorable moisture conditions during early-spring, at the start of the growing season, can promote cambial reactivation after summer dry period and prolong wood formation later into the year (Vieira et al., 2020; Zalloni et al., 2016).

The growth of *P. pinaster* in northern cooler and wetter site might also been shown to be enhanced by broader environmental changes such as the rising temperatures along with increased atmospheric CO_2 concentrations (Allen et al., 2015; Camarero et al., 2021; Férriz et al., 2025; Martínez-Vilalta et al., 2008). However, these factors may only enhance growth rates if water availability is not limited (Allen et al., 2015; Férriz et al., 2025; Peñuelas et al., 2011). In this way, trees in the southern hotter and drier site are less likely to benefit from such interactions.

Despite the absence of significant period effects in yearly TRI in *P. pinea* for the southern site (Table 5), the mean TRI was lower in Period 2 (Table 4, Fig. 9). This pattern can occur because mean TRI integrates growth over multiple years, capturing cumulative or persistent shifts in growth performance that may not be detectable when analyzing year-to-year variability. A possible sustained reduction in growth across several years can therefore appear in the mean TRI even when yearly TRI differences are not statistically significant. This lower mean TRI suggests a reduced growth capacity of *P. pinea* under the warmer and drier conditions that characterize Period 2.

This decline contrasts with *P. pinaster* in the same region, for which no reduction in mean TRI was observed, indicating species-specific responses to warming. Some possibilities may contribute to the reduced growth of *P. pinea* in Period 2. Accordingly, with the results from Nabais et al. (2014) *P. pinea* in southern Portugal may initiate growth earlier in the season. In our study, the positive correlation with January temperatures at the southern site might suggest this tendency toward earlier growth resumption. Yet, an advanced onset of cambial activity does not necessarily translate into increased radial growth (Camarero et al., 2022). In Mediterranean climates, an early growing season is beneficial only when spring moisture remains sufficient (Gao et al., 2022). However, with climate change, spring precipitation has become less frequent and more irregular while autumn precipitation has increased (De Lima et al., 2013; Paulo et al., 2012). Under these conditions, an extended growing season may increase respiratory costs relative to photosynthetic gains, contributing to reduced annual biomass accumulation (Gao et al., 2022).

In addition, some works report an anisohydric strategy for *P. pinea* (Férriz et al., 2023; Ripullone et al., 2007), sustaining gas exchange longer during dry periods. While photosynthesis may continue under moderate drought, growth is more sensitive to water limitation (Körner, 2015; Sarris et al., 2013). As a result, *P. pinea* may halt cambial activity during drought while still losing carbon through respiration.

Particularly as droughts have become more frequent and intense in recent decades and anisohydric responses no necessarily lead to an increase of carbon gains during droughts periods (Kannenberg et al., 2019). If trees enter autumn with depleted carbon reserves, due to sustained summer respiration, their capacity to produce additional latewood cells in the second period of growth is diminished, according to bimodal growth of mediterranean pines. Moreover, while the formation of IADFs in latewood in *P. pinea* may occur mainly until autumn, *P. pinaster* IADFs formation can extend further into winter when conditions allow (Nabais et al., 2014), producing early-wood cells in latewood and contributing to wider rings, consistent with its more opportunistic response of *P. pinaster* to climate.

The capacity of tree to regrow after drought, i.e., growth recovery, is highly dependent on moisture availability after drought (Gazol et al., 2016; Serra-Maluquer et al., 2018; Vergarechea et al., 2021; Veuillen et al., 2023). The same sensitivity to moisture availability in both species under a warming climate (Table 5), suggests that its future drought recovery will largely depend on the specific characteristics of upcoming drought events, such as their intensity, duration, frequency, and impact on local water availability. This pattern is consistent with current perspectives in the Mediterranean, where reduced drought recovery is primarily attributed to site-specific conditions and declining moisture availability (Gazol et al., 2018; Sánchez-Salguero et al., 2018; Vergarechea et al., 2021; Veuillen et al., 2023). Therefore, both species will become more dependent on favorable post-drought conditions to recover from drought and may be more vulnerable to drought-induced mortality. (DeSoto et al., 2020)

Furthermore, the capacity of both of our study species to maintain growth and withstand future drier conditions may be increasingly compromised, especially in the southern region, which is already more water-limited. In these drier environments, trees are more vulnerable to drought (Bose et al., 2020; Leifsson et al., 2024), and current climate–growth correlations reveal a stronger dependence on water availability (Figs. 5 and 6), further underscoring the challenges these populations may face under continued climate change. This could, in turn, limit the ability of these species to persist and expand in the region, potentially leading to shifts in species composition and a decrease in overall forest diversity (Benito-Garzón et al., 2011; 2013).

Our study was conducted in coastal areas, which are generally wetter than inland regions. Mediterranean trees in these coastal sites tend to show more pronounced bimodal growth and a higher occurrence of IADFs (Pacheco et al., 2018; Valeriano et al., 2023), reflecting distinct responses to climate variability. Therefore, extrapolating these findings to inland areas should be made with caution.

5. Conclusion

Our study demonstrates that under ongoing warming trends, water availability has become the dominant factor influencing growth, with both *P. pinaster* and *P. pinea* showing non-stationary responses to climate. Although it was not found an increase in sensitivity to water availability due to non-stationarity, the two species had a different response to warming. Surprisingly, while *P. pinaster* showed an enhanced growth at mesic sites where water was more available, *P. pinea* growth appeared to be reduced in the xeric southern area. This result might lead to a change in the current consideration of these two species capacity for coping with future climate conditions. The capacity of these species to recover from upcoming drought will depend on future drought intensity, duration, frequency, and impact on local water availability.

A deeper understanding of the mechanisms underlying tree responses to drought will be essential for improving the accuracy and effectiveness of forest management strategies under future climate scenarios. Our results underscore the importance of explicitly assessing non-stationary responses to climate in dendroclimatic studies. Determining whether species exhibit stationary or non-stationary climate–growth relationships is essential, as this distinction allows a more accurate identification of differences in drought susceptibility. Not considering non-stationarity may reduce the reliability of models projecting future climate–growth responses, leading to under- or overestimation of species' capacity to cope with warming and drought. Also, because dendroclimatology approaches are widely used to reconstruct past climate, evaluating non-stationary behavior is also critical for identifying the most reliable species for such reconstructions. Ultimately, incorporating non-stationarity into dendroclimatic analyses provides more precise models and might prevent misleading assumptions.

CRediT authorship contribution statement

Joshua J. Puhlick: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Teresa Calvão:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **João Campôa:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carla S. Pimentel:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We gratefully acknowledge the Portuguese forest authority, Instituto da Conservação da Natureza e das Florestas (ICNF), for granting access to the national forests. We particularly acknowledge ICNF Regional Directorate for Centro, for providing the additional 19 stem discs from logged *P. pinaster* trees, and Fernanda Calvão Rodrigues of the ICNF Regional Directorate for Alentejo for the logistical assistance for fieldwork. We also thank Ianize Cardoso for assisting during fieldwork. J. Campôa was funded through a PhD scholarship (2021.05104.BD) funded by the Portuguese Foundation for Science and Technology (FCT); and C. Pimentel through the grant SFRH/BPD/80867/2011 and the contract DL57/2016/CP1382/CT0009. This work was funded by the projects PTDC/BIA-ECO/31655/2017 and PTDC/ASP-SIL/29774/2017 (funded by FCT and by the programs COMPETE 2020 and Portugal 2020 from the European Regional Development Fund (FEDER)). The research units CEF (UID/00239/2025; DOI: https://doi.org/10.54499/UID/00239/2025) and CENSE (UID/PRR/04085/2025; DOI: https://doi.org/10.54499/UID/PRR/04085/2025) and the associated laboratory CHANGE (LA/P/0121/2020; DOI: https://doi.org/10.54499/LA/P/0121/2020) supported this research.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2026.126469.

Data availability

Data will be made available on request.

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